

Summer drought affects abundance of grassland grasshoppers differently along an elevation gradient

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Funding information

Stöckmann Foundation for Environment and Nature Conservation, Grant/Award Number: S0393/10017/2019

Associate Editor: Peter Mayhew

Abstract

1. Orthoptera (hereinafter termed 'grasshoppers') are of great functional significance since they are the main arthropod consumers in grasslands and an important food source for medium-sized insectivorous vertebrates. However, research investigating the effects of extreme weather events on the abundance of grasshoppers has lacked thus far.
2. Here, we studied the effects of summer drought on grasshopper abundance in temperate semi-natural grasslands with low land-use intensity. We considered calcareous and mesic grasslands; per type, we randomly selected 27 plots.
3. Our study revealed distinct differences in habitat characteristics between plots of calcareous and mesic grasslands. Overall, calcareous grasslands had a more heterogeneous and shorter vegetation than mesic grasslands. Consequently, species richness was higher in calcareous grasslands. By contrast, grasshopper abundance did not differ between the two types.
4. Summer temperature was the key driver of grasshopper abundance. Abundance was lowest in grasslands that were situated at lower elevations with higher summer temperatures and that were characterised by the strongest effects of summer drought. Its influence even overrode the differences in habitat characteristics between calcareous and mesic grasslands.
5. Extreme weather events, such as summer droughts, are expected to become more frequent due to global warming. Accordingly, suitable conservation strategies that increase the resistance and resilience of temperate semi-natural grasslands and their insect assemblages against summer drought are highly needed. Based on our study, increasing habitat heterogeneity seems to be the most effective way to mitigate the negative effects of summer drought.

KEYWORDS

biodiversity conservation, climate change, extreme weather event, habitat heterogeneity, insect decline, semi-natural grassland

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INTRODUCTION

During the last two centuries, humankind has modified the environment globally at an unprecedented rate (Foley et al., 2005; Rockström et al., 2009). Accordingly, biodiversity is in sharp decline and scientists suspect that we are heading for a sixth mass extinction (Barnosky et al., 2011; Dirzo et al., 2014). The dramatic loss of species jeopardises ecosystem functioning and human well-being on our planet (Cardoso et al., 2020; Dirzo et al., 2014; IPBES, 2019; Ripple et al., 2017). Therefore, halting the decline is one of the major challenges for humanity.

Insects are the most speciose taxon on earth (Stork, 2018). However, their decline is much faster than those of most other organisms (e.g. plants or vertebrates) (Cardoso et al., 2020; Sánchez-Bayo & Wyckhuys, 2019; Thomas et al., 2004; Wagner, 2020). The loss of insects has cascading effects on various other taxa within ecosystems (Cardoso et al., 2020; Wagner, 2020). For example, the abundance of insect prey is strongly interrelated with the population size of medium-sized insectivorous species at higher trophic levels (e.g. birds) (Fartmann et al., 2021a, 2021b; González del Portillo et al., 2021; Hebda et al., 2019). As has been shown for biodiversity in general, land-use and climate change are the main drivers of declines in insects too (Cardoso et al., 2020; IPBES, 2019; Wagner, 2020).

Nutrient-poor semi-natural grasslands belong to the most species-rich ecosystems across Europe (Chytrý et al., 2015; Dengler et al., 2014; Feurdean et al., 2018). However, with ongoing industrialisation of agricultural land use, their area has strongly declined (Fartmann et al., 2021a, 2021b; Poschlod & Braun-Reichert, 2017; WallisDeVries et al., 2002). Additionally, the remaining grassland patches have often suffered from habitat deterioration, mainly due to land-use intensification and abandonment. More recently, global warming has become another significant threat for grassland biodiversity (De Keersmaecker et al., 2016; Fischer et al., 2020; Vogel et al., 2012).

Orthoptera (hereinafter termed 'grasshoppers') are of great functional significance since they are the main arthropod consumers in grasslands (Samways, 2005) and an important food source for insectivorous vertebrates (Fartmann et al., 2021a, 2021b; González del Portillo et al., 2021; Hebda et al., 2019; Ingrisch & Köhler, 1998). This is also true for Central Europe, where grasshopper assemblages are usually species-poor but certain species may have a high abundance (Ingrisch & Köhler, 1998). Moreover, they respond rapidly to alterations in land use (Uchida & Ushimaru, 2014; Theron et al., 2022) and climate (Fumy et al., 2020; Löffler et al., 2019; Poniatowski et al., 2020). Consequently, they are well-established bioindicators for environmental change in grassland ecosystems (Fartmann et al., 2012; Sergeev, 2021). Recent studies from Western and Central Europe revealed combined effects of land use and climate change on grasshopper assemblage composition in temperate grasslands (Beckmann et al., 2015; Poniatowski et al., 2012, 2020; Löffler et al., 2019, 2020; Fumy et al., 2020; Fartmann et al., 2021a, 2021b). By contrast, research investigating the effects of extreme weather events (e.g., summer droughts, which are characteristic results of global warming; IPCC, 2021) on the abundance of grasshoppers has lacked thus far.

Here, we studied the effects of summer drought on grassland grasshoppers across an elevation gradient within a Central European landscape (Figure 1). We considered calcareous and mesic grasslands; for each grassland type, we randomly selected 27 rectangular plots with a total size of 500 m². We compared the composition of grasshopper assemblages and environmental conditions between the two grassland types at the habitat and landscape level. Moreover, we identified the key drivers of grasshopper abundance. Based on our results, we derived evidence-based conservation measures to increase the resistance and resilience of grasshopper assemblages to summer drought in temperate semi-natural grasslands.

MATERIAL AND METHODS

Study area

The study area, the Diemel Valley (100–600 m a.s.l.), has an area of about 460 km² and is located at the border of the German federal states of North Rhine-Westphalia and Hesse (Central Germany, Figure 1). It exhibits ~750 ha of semi-dry calcareous grasslands and ~250 ha of nutrient-poor mesic grasslands (Fartmann, 2004). The climate is suboceanic (Müller-Wille, 1981). Annual precipitation increases with elevation from 732 to 948 mm, while annual temperature decreases from 8.8°C to 7.9°C (long-term mean: 1981–2010; weather station: Warburg [236 m a.s.l.] and Brilon [447 m a.s.l.], respectively; German Meteorological Service, 2021). In order to account for possible spatial autocorrelation, the study area was divided into seven subareas according to elevation and landscape configuration (Figure 1).

Large parts of Central Europe, including the study area, were characterised by severe summer droughts in 2018 and 2019 as a result of substantial rainfall deficits and heat waves (Boergens et al., 2020; European Drought Observatory, 2021). In 2020 (the study year), spring and early summer (April–July) were also warmer and drier than average. During that period temperatures were 0.43°C (weather station: Warburg) and 0.70°C (weather station: Brilon) higher, respectively (reference: long-term mean 1981–2010; German Meteorological Service, 2021). The rainfall deficit was most pronounced in the drier lower elevations of the study area, reaching only 53% of the average values (weather station: Warburg); the wetter upper elevations experienced 76% of the long-term mean (weather station: Brilon). As a result, in lower elevations of the study area, vegetation of calcareous grasslands and even those of mesic grasslands partly started to wither already in June (own observation; see also Fischer et al., 2020). By contrast, in upper elevations of the study area, grassland plants were still vital at that time.

Sampling design

Plots

We studied two types of semi-natural grasslands with low land-use intensity: (i) semi-dry calcareous grasslands (*Gentiano-Koelerietum*) and

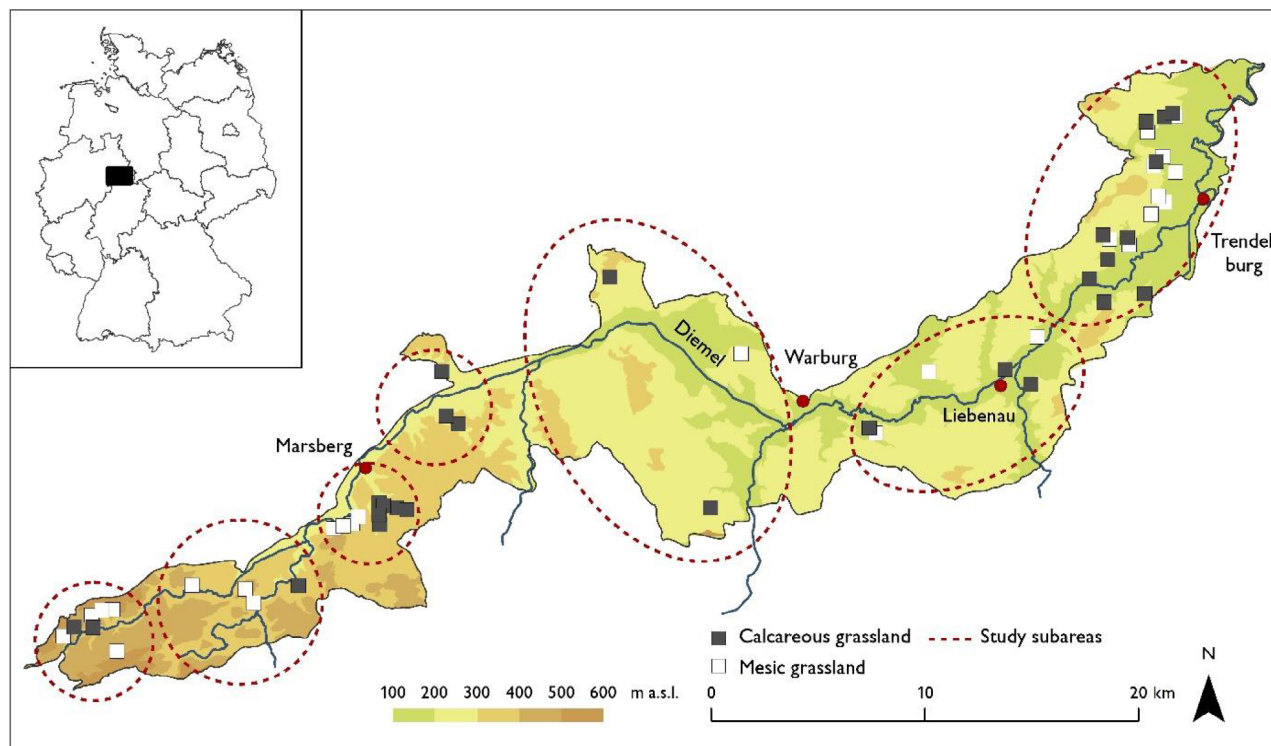


FIGURE 1 Location of the Diemel Valley and plots in Central Germany

(ii) nutrient-poor mesic grasslands (*Arrhenatheretum* and nutrient-poor stands of the *Lolio-Cynosuretum*) (Figure 2) (Fartmann, 2004). For each grassland type, we randomly selected 27 rectangular plots with a total size of 500 m² within a randomly chosen grassland patch across the elevation gradient of the study area ($N = 54$) (Figure 1).

Environmental conditions

Macroclimate

Characteristics of the local climate of each plot (mean summer [April–September] precipitation and temperature) were derived from 1-km² grid datasets of Germany (German Meteorological Service, 2021) that contain 10-year (2010–2019) mean values (Table 1). The mean elevation (m a.s.l.) of the plots was calculated from topographic maps using ArcGIS 10.2.

Landscape and habitat characteristics

For each plot, we assessed several parameters of landscape and habitat characteristics (Table 1). The parameters of landscape characteristics ‘patch size’ and ‘connectivity’ were determined on the basis of aerial photographs using ArcGIS 10.2. We measured the connectivity of the focal patch as the geometric mean of the edge-to-edge distance to the three nearest patches (Eichel & Fartmann, 2008; Scherer et al., 2021). Distances from the focal patch to the three other patches

were computed using the proximity-analysis tool ‘near table’ in ArcGIS 10.2.

We sampled parameters of habitat characteristics within the plot once in mid-June 2020 (Table 1). In each plot, we ascertained environmental parameters in a randomly selected undisturbed part of the plot with a size of 3 × 3 m. We recorded the following parameters of horizontal vegetation structure with an accuracy of 5%: cover of shrubs, field layer, grasses, herbs, mosses, litter, bare ground and gravel. In cases in which cover was above 95% or below 5%, 2.5% steps were used. To calculate habitat heterogeneity, we counted the number of the following habitat layers: shrubs, grasses, herbs, mosses, litter, bare ground and gravel. We only considered layers with a minimum cover of 5%. As a result, the values of the habitat-heterogeneity score in our study ranged between 2 and 5 per plot. Furthermore, vertical vegetation structure was ascertained by measuring vegetation height at an accuracy of 2.5 cm. Land use was classified into the three categories ‘pasture’, ‘meadow’ and ‘abandoned grassland’.

Grasshopper sampling

Grasshopper assemblages were recorded in each plot using a box quadrat (1.41 × 1.41 m \triangleq 2.0 m²), which ranks among the most accurate sampling methods to ascertain species richness and abundance of grasshoppers (Gardiner & Hill, 2006). To avoid edge effects (Schirmel et al., 2010), the box quadrat was randomly dropped at 10 different points in the centre of the plot, covering a total area of 20 m² per plot (Fartmann et al., 2012; Poniatowski & Fartmann, 2008). Sampling

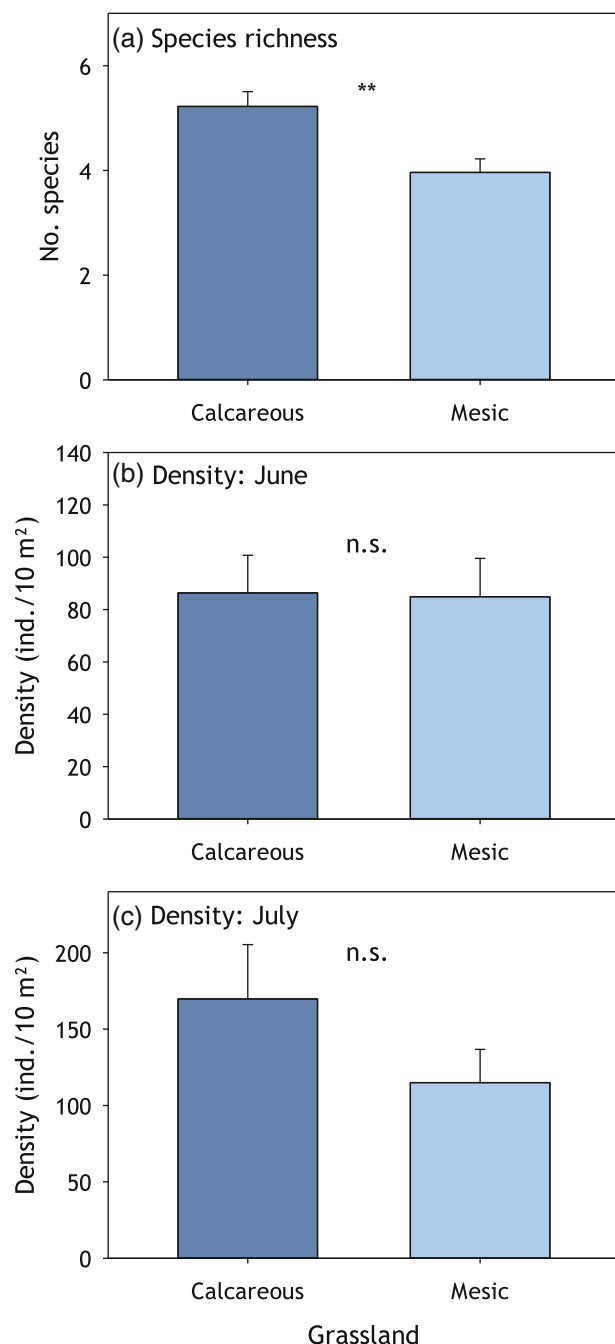


FIGURE 2 Mean values (\pm SE) of grasshopper species richness (a) and grasshopper densities (June (b), July (c)) in plots of calcareous and mesic grasslands ($N = 54$). Differences between the grassland types were analysed using GLMMs with 'subarea' as a random factor. n.s., not significant, $p > 0.05$; ** $p \leq 0.01$, *** $p \leq 0.001$

occurred twice per plot: in mid-June (mainly nymphs) and mid-July (mainly adults), which is the phenology peak of nymphs and adults, respectively, in Central Europe (Ingrisch & Köhler, 1998). Within the box quadrat, grasshoppers were captured by sweep netting and hand. Species identification was done in the field using Fischer et al. (2020). The scientific nomenclature of the species follows Fischer et al. (2020).

TABLE 1 Overview of sampled predictor parameters (mean \pm SE; $N = 54$).

	Grassland type		
Parameter	Calcareous	Mesic	<i>p</i>
Macroclimate			
Elevation a.s.l. (m)	269 ± 14	293 ± 21	n.s.
Summer precipitation (mm) ^a	396 ± 5	412 ± 7	n.s.
Summer temperature (°C) ^a	13.9 ± 0.1	13.7 ± 0.1	n.s.
Landscape characteristics			
Patch size (ha)	9.9 ± 2.0	12.3 ± 2.9	n.s.
Patch connectivity (m) ^b	1580 ± 411	1133 ± 232	n.s.
Habitat characteristics			
Habitat structure			
Cover (%)			
Shrubs	3.7 ± 1.1	0.4 ± 0.2	***
Field layer			
Grasses	78.6 ± 5.5	86.8 ± 8.1	n.s.
Herbs	46.1 ± 2.6	54.4 ± 4.4	n.s.
Mosses	32.5 ± 2.9	32.3 ± 3.7	n.s.
Litter	3.3 ± 0.8	2.4 ± 1.2	*
Bare ground	12.4 ± 1.7	11.1 ± 2.1	n.s.
Gravel	9.3 ± 1.1	5.2 ± 1.0	*
	1.1 ± 0.5	0.5 ± 0.4	*
Habitat heterogeneity	3.30 ± 0.14	2.52 ± 0.20	**
Vegetation height (cm)	10.5 ± 1.0	25.4 ± 2.8	***

Note: Differences between the grassland types were analysed using GLMMs with 'subarea' as a random factor. Significant differences are indicated by bold type. n.s., not significant, $p > 0.05$; * $p \leq 0.05$; ** $p \leq 0.01$; *** $p \leq 0.001$.

^aApril–September.

^bDistance to the three nearest patches (geometric mean).

Statistical analysis

All statistical analyses were performed using R 3.4.1 (R Core Team, 2021). For all generalised linear mixed-effects models (GLMMs) (R packages lme4; Bates et al., 2021) the variable 'subarea' was used as a random factor (Crawley, 2007).

To detect differences in land use between plots of calcareous and mesic grasslands, we conducted a χ^2 test. To identify indicator species for each grassland type, an indicator-species analysis (de Cáceres & Jansen, 2016; Dufrêne & Legendre, 1997) was carried out using grasshopper data from both sampling periods (June and July). Differences in metric environmental parameters (Table 1) as well as in species richness (pooled for both sampling periods) (Figure 2) and abundance (separately for June and July) (Figure 2) between calcareous and mesic grasslands were analysed using GLMMs. Grassland type served as a nominal fixed factor (predictor), and the analysed parameters were used as dependent variables. Depending on the distribution of the variables, proportional binomial (percentage data), Poisson (count data) or Gaussian (for square-root- or log-transformed variables with normal distribution) models were applied with the respective standard

TABLE 2 Absolute and relative frequencies of the nominal variable 'land use' in plots of calcareous ($N = 27$) and Mesic grasslands ($N = 27$)

Parameter	Grassland type				χ^2	df	p
	Calcareous		Mesic				
	Absolute	%	Absolute	%			
Land use					10.36	2	**
Pasture	24	88.9	20	74.1			
Meadow	0	0	7	25.9			
Abandoned	3	11.1	0	0			

Note: Comparison between groups was done by χ^2 test. ** $p \leq 0.01$.

link functions. To reduce overdispersion within the models (proportional binomial/Poisson), observation-level random effects were added as another random factor (Harrison, 2014, 2015). The overall effect of the dependent variables on grassland type was analysed by comparing the full models with reduced models without 'grassland type' as the fixed factor and by applying likelihood-ratio tests.

GLMMs (negative-binomial) were calculated to detect those environmental parameters that explain the abundance of grasshoppers in the two grassland types. To avoid model over-fitting, strongly intercorrelated (Spearman rank correlation [r_s]; $|r_s| > 0.5$) variables were excluded and only the most important variable was used in GLMM analyses (Tables A2 and A3) (cf. Löffler & Fartmann, 2017). Therefore, for the plots of calcareous grasslands, patch connectivity, elevation, shrubs, field layer, herbs and litter were excluded from the GLMM analyses (Table A2). For the plots of mesic grasslands, elevation, summer precipitation, field layer, grasses, gravel, habitat heterogeneity and vegetation height were not entered into the models (Table A3). In order to increase model robustness and identify the most important environmental parameters, we conducted model averaging based on an information-theoretic approach (Burnham & Anderson, 2002; Grueber et al., 2011). Model averaging was done using the dredge function (R package MuMIn; Bartón, 2021) and included only top-ranked models within $\Delta AIC_c < 3$ (Grueber et al., 2011).

RESULTS

Environmental conditions

Habitat characteristics differed, in contrast to macroclimate and landscape characteristics, between plots of calcareous and mesic grasslands (Table 1). Overall, plots of calcareous grasslands had a more heterogeneous and shorter vegetation than those of mesic grasslands. Moreover, the cover of shrubs, mosses, bare ground and gravel was higher. Land use also differed (Table 2). Pastures clearly dominated in both grassland types. However, one-tenth of the plots of calcareous grasslands were abandoned and a quarter of the plots of mesic grasslands were used as a meadow. By contrast, the other sampled parameters of habitat characteristics did not differ between the two grassland types.

TABLE 3 Results of indicator species analysis (ISA) (de Cáceres & Jansen, 2016; Dufrêne & Legendre, 1997) for plots of calcareous and mesic grasslands based on grasshopper densities in June and July ($N_{\text{plots}} = 54$)

Species	IV	p	Grassland type	
			Calcareous	Mesic
<i>Chorthippus albomarginatus</i>	5.6	n.s.	25/4	75/7
<i>Chorthippus biguttulus</i>	72.8	**	73/100	27/93
<i>Chorthippus brunneus</i>	11.1	n.s.	100/11	0/0
<i>Chrysocraon dispar</i>	2.0	n.s.	45/4	55/4
<i>Decticus verrucivorus</i>	3.7	n.s.	100/4	0/0
<i>Metrioptera brachyptera</i>	33.5	***	90/37	10/4
<i>Myrmeleotettix maculatus</i>	2.8	n.s.	25/7	75/4
<i>Omocestus viridulus</i>	13.2	n.s.	29/22	71/19
<i>Phaneroptera falcata</i>	34.0	*	83/41	17/15
<i>Pholidoptera griseoaptera</i>	24.4	n.s.	18/19	82/30
<i>Pseudochorthippus parallelus</i>	70.6	**	21/85	79/89
<i>Roeseliana roeselii</i>	33.1	**	19/7	81/41
<i>Stenobothrus lineatus</i>	86.9	***	90/96	10/37
<i>Stenobothrus stigmaticus</i>	6.5	n.s.	12/4	88/7
<i>Tetrix bipunctata</i>	17.5	n.s.	95/19	5/4
<i>Tetrix tenuicornis</i>	32.9	n.s.	64/52	36/19
<i>Tettigonia cantans</i>	14.8	n.s.	0/0	100/15
<i>Tettigonia viridissima</i>	6.9	n.s.	38/11	63/11

Note: IV, indicator value; relative abundance comparing the two grassland types/relative frequency (percentage of plots within each grassland type with occurrence of the species). Grey-hatched: species are indicator species for this grassland type. Significant values are indicated in bold type. n.s., not significant, $p > 0.05$; ** $p \leq 0.01$; *** $p \leq 0.001$.

Grasshopper assemblages and response to environmental conditions

Altogether, we caught 12,313 grasshopper individuals, 8666 nymphs and 3647 adults, belonging to 18 species during the two sampling periods (Table A1). The most widespread species were *Chorthippus biguttulus* and *Pseudochorthippus parallelus*, accounting for 59% and 25%, respectively, of all individuals. The ratio of nymphs to adults was 13.8: 1 in June and 1: 2.1 in July. Plots of calcareous grasslands had a

TABLE 4 Model-averaging results (GLMM; negative binomial error structure): Relationship between grasshopper densities in June (a, c, e) and July (b, d, f), respectively, and environmental parameters in plots of calcareous grasslands ($N = 27$)

Parameter	Estimate	SE	Z	p
1. Landscape model				
(a) June ($R^2_m = 0.61$, $R^2_c = 0.61$)				
(Intercept)	32.06	9.45	3.30	***
Summer temperature	-1.78	0.50	3.42	***
Summer precipitation	-0.01	0.01	1.94	n.s.
(b) July ($R^2_m = 0.42$ -0.44, $R^2_c = 0.42$ -0.44)				
(Intercept)	20.75	6.64	3.00	**
Summer temperature	-1.18	0.40	2.82	**
Summer precipitation	-0.00	0.00	0.43	n.s.
2. Habitat model				
(c) June ($R^2_m = 0.36$ -0.39, $R^2_c = 0.65$ -0.66)				
(Intercept)	4.15	0.70	5.71	***
Habitat heterogeneity	0.22	0.18	1.18	n.s.
Bare ground	0.04	0.04	0.81	n.s.
Mosses	-0.03	0.03	0.94	n.s.
Vegetation height	-0.03	0.02	1.08	n.s.
(d) July ($R^2_m = 0.21$ -0.40, $R^2_c = 0.56$ -0.63)				
(Intercept)	3.45	0.58	5.80	***
Habitat heterogeneity	0.26	0.17	1.45	n.s.
Bare ground	0.05	0.02	1.81	n.s.
Mosses	-0.04	0.03	1.25	n.s.
Gravel	-0.05	0.05	1.04	n.s.
3. Synthesis model				
(a) June ($R^2_m = 0.45$, $R^2_c = 0.49$)				
(Intercept)	23.64	5.59	4.23	***
Summer temperature	-1.40	0.40	-3.47	***
(b) July ($R^2_m = 0.34$, $R^2_c = 0.40$)				
(Intercept)	18.63	4.79	3.89	***
Summer temperature	-1.08	0.35	-3.13	**

Note: Model-averaged coefficients (conditional average) were derived from the top-ranked models ($\Delta AIC_C < 3$). R^2_m , variance explained by fixed effects; R^2_c , variance explained by both fixed and random effects (Nakagawa et al., 2017). n.s., not significant, $p > 0.05$; ** $p \leq 0.01$; *** $p \leq 0.001$.

higher species richness than those of mesic grasslands (Figure 2). By contrast, grasshopper densities (June and July) did not differ between the two grassland types.

Both grassland types were characterised by indicator species (Table 3). *Chorthippus biguttulus*, *Metrioptera brachyptera*, *Phaneroptera falcata* and *Stenobothrus lineatus* were indicative for plots of calcareous grasslands. By contrast, *Pseudochorthippus parallelus* and *Roeseliana roeselii* were characteristic of plots of mesic grasslands.

Summer temperature was the key driver of grasshopper abundance in the GLMM analyses (Tables 4 and 5, Figure 3). In both grassland types and in both types of models (landscape and synthesis model), abundance (June and July) was lowest in plots that were situated at lower elevations with higher summer temperatures (for

intercorrelations of the two variables, see Tables A2 and A3). In plots of calcareous grasslands, none of the habitat characteristics affected grasshopper abundance (Table 4). In plots of mesic grasslands, additionally, the cover of herbs, which was negatively correlated with the cover of grasses (Table A3), had a positive effect in the habitat (June and July) and synthesis model (July) (Table 5, Figure 3).

DISCUSSION

Our study revealed distinct differences in habitat characteristics between plots of calcareous and mesic grasslands. Overall, calcareous grasslands had a more heterogeneous and shorter vegetation than mesic grasslands. Consequently, species richness was higher in

TABLE 5 Model-averaging results (GLMM; negative binomial error structure): relationship between grasshopper densities in June (a, c, e) and July (b, d, f), respectively, and environmental parameters in plots of mesic grasslands ($N = 27$)

Parameter	Estimate	SE	Z	p
1. Landscape model				
(a) June ($R^2_m = 0.32$, $R^2_c = 0.23$ – 0.32)				
(Intercept)	9.72	4.65	2.05	*
Summer temperature	−0.60	0.23	2.45	*
Patch size	0.02	0.01	1.39	n.s.
Patch connectivity	−0.00	0.00	0.72	n.s.
(b) July ($R^2_m = 0.37$, $R^2_c = 0.32$ – 0.37)				
(Intercept)	0.14	2.97	4.40	***
Summer temperature	−0.74	0.22	3.25	**
Patch size	0.01	0.01	0.62	n.s.
Patch connectivity	−0.00	0.00	0.20	n.s.
2. Habitat model				
(c) June ($R^2_m = 0.26$, $R^2_c = 0.30$ – 0.50)				
(Intercept)	3.53	0.48	7.04	***
Herbs	0.02	0.01	2.00	*
Bare ground	−0.06	0.04	1.47	n.s.
(d) July ($R^2_m = 0.16$ – 0.21 , $R^2_c = 0.55$ – 0.56)				
(Intercept)	2.93	0.40	6.99	***
Herbs	0.02	0.01	2.40	*
Bare ground	−0.03	0.02	1.43	n.s.
Mosses	−0.01	0.02	0.40	n.s.
3. Synthesis model				
(e) June ($R^2_m = 0.35$, $R^2_c = 0.25$ – 0.42)				
(Intercept)	7.14	4.94	1.43	n.s.
Summer temperature	−0.65	0.24	2.56	*
Herbs	0.01	0.01	1.60	n.s.
(f) July ($R^2_m = 0.37$ – 0.47 , $R^2_c = 0.37$ – 0.50)				
(Intercept)	8.52	5.85	1.45	n.s.
Summer temperature	−0.78	0.21	3.55	***
Herbs	0.02	0.01	2.03	*

Note: Model-averaged coefficients (conditional average) were derived from the top-ranked models ($\Delta AIC_C < 3$). R^2_m , variance explained by fixed effects; R^2_c , variance explained by both fixed and random effects (Nakagawa et al., 2017). n.s., not significant, $p > 0.05$; * $p \leq 0.05$; ** $p \leq 0.01$; *** $p \leq 0.001$.

calcareous grasslands. Surprisingly, however, grasshopper abundance did not differ between the two grassland types. Summer temperature was the key driver of grasshopper abundance. Abundance was statistically lowest in grasslands that were situated at lower elevations with higher summer temperatures.

All 18 detected grasshopper species in this study are characteristic of grassland in Central Europe (Detzel, 1998; Poniatowski & Fartmann, 2008; Schlumprecht & Waeber, 2003; Schulte, 2003). Additionally, the observed habitat preferences of the species, indicated by the indicator species analysis, were also in line with literature. In particular, *M. brachyptera* and *S. lineatus* are known to exhibit strong preferences for calcareous grasslands, and *P. parallelus* and *R. roeselii* for mesic grasslands.

Calcareous grasslands are well-known for their high biodiversity, especially richness of specialised plant and insect species (Diacon-Bolli et al., 2012; Krämer et al., 2012; Poniatowski & Fartmann, 2008; WallisDeVries et al., 2002). In line with this, compared with mesic grasslands, calcareous grasslands had a higher overall grasshopper species richness and more indicator species. We attribute this finding to greater heterogeneity within plots of calcareous grasslands, exhibiting a higher cover of shrubs, mosses, bare ground and gravel (cf. Löffler & Fartmann, 2017; Schwarz & Fartmann, 2022).

Despite the differences in habitat characteristics, grasshopper abundance did not differ between calcareous and mesic grasslands. Grasshoppers are ectothermic organisms whose development time, fecundity and lifespan critically depend on temperature (Chappell &

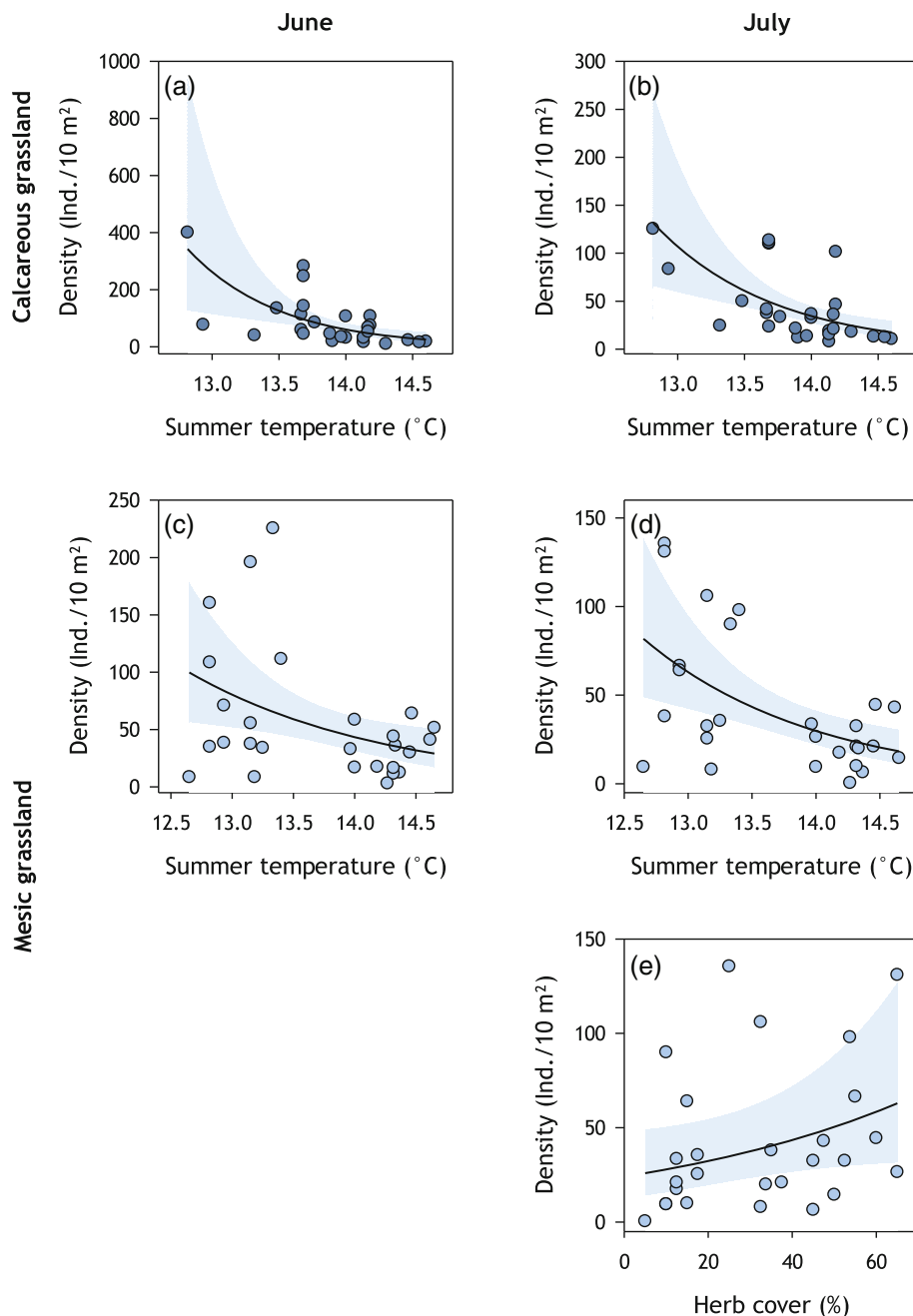


FIGURE 3 Relationship between grasshopper densities in June (a, c) and July (b, d, e), respectively, and significant environmental parameters of the synthesis models in plots of calcareous grasslands (a and b, $N = 27$) and of mesic grasslands (c–e, $N = 27$) (see Tables 4 and 5 for detailed GLMM statistics). Blue hatching indicates 95% confidence intervals

Whitman, 1990; Willott & Hassall, 1998). Macroclimatic conditions did not differ in our study between plots of the two grassland types. By contrast, in both grassland types, summer temperature decreased consistently with elevation. In the GLMM analyses, it was the most important predictor and had a negative effect on grasshopper abundance. Up to now, usually the opposite was observed in temperate grasslands; that is, high temperatures foster high grasshopper population densities (Fartmann et al., 2012; Gardiner & Dover, 2008; Löffler & Fartmann, 2017). However, we have to consider that the study year was the third consecutive year with a summer drought,

which is rather unusual for temperate regions in general and the study area in particular (see Section 2.1). As a result, in the lower elevations of the study area, vegetation of both grassland types started to wither already in June. Therefore, we interpret the negative relationship between summer temperature and grasshopper abundance as being caused by food shortage for the mostly herbivorous grasshoppers. For regions regularly characterised by summer drought, such as the Mediterranean area, food availability has also been identified as an important limiting factor of grasshopper population density (Löffler et al., 2016).

In mesic grasslands, the cover of herbs was an additional predictor. Abundance of grasshoppers increased with the cover of herbs, which was a surrogate for a low cover of grasses and vice versa, since both variables were negatively correlated. Usually, a narrow grass-herb ratio in grasslands is a surrogate for low land-use intensity and high phytodiversity (Ellenberg & Leuschner, 2010; Löffler & Fartmann, 2017). By contrast, more intensive management (e.g., grazing several times per year with high stocking rates) promotes a few competitive grasses at the expense of herbs (wide grass-herb ratio) and more uniform stands (Dierschke & Briemle, 2002; Ellenberg & Leuschner, 2010; Grime et al., 2007). In mesic grasslands of the study area, *Agrostis capillaris*, *Cynosurus cristatus*, *Festuca rubra* agg. or *Lolium perenne* are characteristic species benefiting from more intensive land use (Fartmann, 2004). A higher land-use intensity is known to have detrimental effects on grassland grasshoppers (Fumy et al., 2021). Each management event may cause direct mortality of grasshoppers and increases the risk of predation through insectivorous vertebrates in the short swards (Humbert et al., 2012; Wünsch et al., 2012; Buri et al., 2013). Additionally, species-rich grasslands with a low land-use intensity are known to be more resistant to summer drought (De Keersmaecker et al., 2016; Vogel et al., 2012).

In conclusion, the effects of summer drought were the most likely driver of grasshopper abundance in both grassland types. Its influence even overrode the differences in habitat characteristics between calcareous and mesic grasslands. Extreme weather events, such as summer droughts, are expected to become more frequent due to global warming (IPCC, 2021). Accordingly, suitable conservation strategies that increase the resistance and resilience of temperate semi-natural grasslands and their insect assemblages against summer drought are highly needed.

IMPLICATIONS FOR CONSERVATION

Grasshoppers are key organisms in grassland ecosystems (Fartmann et al., 2021a, 2021b; González del Portillo et al., 2021; Hebda et al., 2019; Samways, 2005). Based on our study, increasing habitat heterogeneity in semi-natural grasslands seems to be the most effective way to mitigate the negative effects of summer drought on grasshopper assemblages. Hence, we recommend preserving and creating mosaics of heterogeneous vegetation with varying sward heights, interspersed shrubs and some solitary trees within the grasslands (cf. Hartel & Plieninger, 2014; Jakobsson et al., 2020; Kindvall, 1996; Plieninger et al., 2015; Schwarz & Fartmann, 2022). For regions with regular summer drought, it has been shown that wood pastures, such as the 'dehesa' in Spain or the 'montado' in Portugal, sustain overall biodiversity and insect abundance (Hartel & Plieninger, 2014; Plieninger et al., 2015). Both low-intensity rough grazing and year-round grazing systems with low stocking rates seem to be suitable tools to increase the heterogeneity in the studied grasslands (Fraser et al., 2014; Köhler et al., 2016; Olff et al., 1999). In mesic grasslands, a quarter of the plots were used as a meadow.

Since mowing results in short homogeneous swards directly after the management event and thereby causes increased predation of insects, pastures should generally be preferred over meadows. Moreover, conservation management should aim to restore calcareous and mesic grasslands on north- and east-facing slopes (Stuhldreher & Fartmann, 2018). This would enable the species to accommodate extreme weather events to some degree without moving to other habitat patches. Such measures are also assumed to increase overall grassland biodiversity (Bonari et al., 2017; Diacon-Bolli et al., 2012; Stuhldreher & Fartmann, 2018) and, accordingly, enhance the resistance and resilience of the grassland ecosystems against global warming (De Keersmaecker et al., 2016; Vogel et al., 2012).

ACKNOWLEDGEMENTS

This study was funded by the Stöckmann Foundation for Environment and Nature Conservation (grant: S0393/10017/2019). Open access funding was enabled and organised by the project DEAL. The authors would like to thank two anonymous reviewers for their valuable comments on a previous version of the manuscript.

CONFLICTS OF INTEREST

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from Stöckmann Foundation for Environment and Nature Conservation. Restrictions apply to the availability of these data, which were used under license for this study.

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How to cite this article: Fartmann, T., Brüggeshemke, J., Poniatowski, D. & Löffler, F. (2022) Summer drought affects abundance of grassland grasshoppers differently along an elevation gradient. *Ecological Entomology*, 47(5), 778–790. Available from: <https://doi.org/10.1111/een.13168>

APPENDIX

TABLE A1 List of grasshopper species recorded in the study area

Species	Number of individuals		
	Nymphs	Adults	Sum
<i>Chorthippus albomarginatus</i>	0	8	8
<i>Chorthippus biguttulus</i>	5668	1558	7226
<i>Chorthippus brunneus</i>	0	8	8
<i>Chrysochraon dispar</i>	3	8	11
<i>Decticus verrucivorus</i>	0	2	2
<i>Metrioptera brachyptera</i>	6	25	31
<i>Myrmeleotettix maculatus</i>	5	3	8
<i>Omocestus viridulus</i>	75	46	121
<i>Phaneroptera falcata</i>	31	11	42
<i>Pholidoptera griseoptera</i>	35	27	62
<i>Pseudochorthippus parallelus</i>	1930	1152	3082
<i>Roeseliana roeselii</i>	57	71	128
<i>Stenobothrus lineatus</i>	474	406	880
<i>Stenobothrus stigmaticus</i>	355	232	587
<i>Tetrix bipunctata</i>	1	18	19
<i>Tetrix tenuicornis</i>	6	68	74
<i>Tettigonia cantans</i>	4	4	8
<i>Tettigonia viridissima</i>	16	0	16
Sum	8666	3647	12,313

TABLE A2 Results of Spearman rank correlations (r_s) of environmental variables in plots of calcareous grasslands

Variable	Conn.	Elev.	Temp.	Shrubs	Field	Grasses	Herbs	Litter	Bare	Hab.	Height
Patch size	-0.67***	-0.20 ^{n.s.}	0.42 ^{n.s.}	0.26 ^{n.s.}	-0.17 ^{n.s.}	0.14 ^{n.s.}	-0.20 ^{n.s.}	0.14 ^{n.s.}	-0.24 ^{n.s.}	0.16 ^{n.s.}	-0.11 ^{n.s.}
Connectivity (Conn.)	/	-0.09 ^{n.s.}	-0.02 ^{n.s.}	-0.16 ^{n.s.}	0.20 ^{n.s.}	0.10 ^{n.s.}	-0.07 ^{n.s.}	-0.15 ^{n.s.}	0.07 ^{n.s.}	-0.11 ^{n.s.}	0.01 ^{n.s.}
Elevation (Elev.)		/	-0.84***	-0.38 ^{n.s.}	0.31 ^{n.s.}	-0.25 ^{n.s.}	0.28 ^{n.s.}	0.20 ^{n.s.}	0.11 ^{n.s.}	-0.21 ^{n.s.}	-0.28 ^{n.s.}
Temperature (Temp.)			/	0.32 ^{n.s.}	0.04 ^{n.s.}	0.34 ^{n.s.}	-0.30 ^{n.s.}	-0.07 ^{n.s.}	-0.31 ^{n.s.}	0.06 ^{n.s.}	0.37 ^{n.s.}
Shrubs				/	-0.28 ^{n.s.}	0.03 ^{n.s.}	-0.14 ^{n.s.}	-0.07 ^{n.s.}	-0.01 ^{n.s.}	0.34 ^{n.s.}	0.59**
Field layer (Field)					/	0.30 ^{n.s.}	0.21 ^{n.s.}	0.08 ^{n.s.}	-0.65***	-0.60**	0.04 ^{n.s.}
Grasses						/	-0.76***	-0.13 ^{n.s.}	-0.28 ^{n.s.}	-0.19 ^{n.s.}	-0.12 ^{n.s.}
Herbs							/	-0.05 ^{n.s.}	0.06 ^{n.s.}	-0.05 ^{n.s.}	0.20 ^{n.s.}
Litter								/	-0.56**	-0.11 ^{n.s.}	0.21 ^{n.s.}
Bare ground (Bare)									/	0.31 ^{n.s.}	-0.15 ^{n.s.}
Habitat hetero. (Hab.)										/	-0.08 ^{n.s.}

Note: Only intercorrelated variables are displayed. Variables with strong intercorrelations ($|r_s| \geq 0.5$) are highlighted in bold.

$p > 0.05$; ** $p \leq 0.01$; *** $p \leq 0.001$.

Abbreviations: Habitat hetero., habitat heterogeneity; height, vegetation height; n.s., not significant.

TABLE A3 Results of Spearman rank correlations (r_s) of environmental variables in plots of mesic grasslands

Variable	Elev.	Precip.	Temp.	Field	Grasses	Herbs	Bare	Gravel	Hab.	Height
Patch size	−0.23 ^{n.s.}	−0.11 ^{n.s.}	0.06 ^{n.s.}	−0.06 ^{n.s.}	−0.20 ^{n.s.}	0.25 ^{n.s.}	0.23 ^{n.s.}	−0.21 ^{n.s.}	0.17 ^{n.s.}	−0.31 ^{n.s.}
Elevation (Elev.)	/	0.79***	−0.92***	0.06 ^{n.s.}	0.09 ^{n.s.}	0.01 ^{n.s.}	−0.16 ^{n.s.}	−0.00 ^{n.s.}	−0.58**	−0.19 ^{n.s.}
Precipitation (Precip.)		/	−0.87***	0.20 ^{n.s.}	0.18 ^{n.s.}	−0.07 ^{n.s.}	−0.25 ^{n.s.}	−0.17 ^{n.s.}	−0.43*	0.09 ^{n.s.}
Temperature (Temp.)			/	−0.09 ^{n.s.}	−0.19 ^{n.s.}	0.10 ^{n.s.}	0.18 ^{n.s.}	−0.17 ^{n.s.}	0.55**	0.08 ^{n.s.}
Field layer (Field)				/	0.47*	0.04 ^{n.s.}	−0.79***	−0.48*	−0.63***	0.58**
Grasses					/	−0.77***	−0.54**	−0.42*	−0.23 ^{n.s.}	0.51**
Herbs						/	0.11 ^{n.s.}	0.06 ^{n.s.}	−0.08 ^{n.s.}	−0.34 ^{n.s.}
Bare ground (Bare)							/	0.52**	0.48*	−0.66***
Gravel								/	0.20 ^{n.s.}	−0.42*
Habitat hetero. (Hab.)									/	−0.38 ^{n.s.}

Note: Only intercorrelated variables are displayed. Variables with strong intercorrelations ($|r_s| \geq 0.5$) are highlighted in bold. $p > 0.05$; ** $p \leq 0.01$; *** $p \leq 0.001$. Abbreviations: Habitat hetero., habitat heterogeneity; height, vegetation height; n.s., not significant.